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BIODIVERSITY AND ECOSYSTEM FUNCTION AND THE DESIGN OF
TALLGRASS RESTORATIONS FOR BIOMASS PRODUCTION

An Abstract of a Thesis
Submitted
in Partial Fulfillment
of the Requirements for the Degree
Master of Science

Dustin Robert Jon Graham
University of Northern Iowa
May, 2015

ABSTRACT

Biodiversity and ecosystem function research (BEF) suggests species richness may provide high levels of ecosystem functions. However, few studies have applied a BEF perspective of restoration, which utilizes biodiversity to achieve increases in ecosystem functions. In this study, we test the application of the BEF perspective of restoration in the design of tallgrass prairie plantings as a biomass crops. Specifically, we examine the effects of planted species richness on biomass production, resistance to disturbance, and resistance to invasion by weeds.

Four seed mixes which range in species richness (1, 5, 16 and 32 species) were established in four, field-scale (0.33-0.55 ha) plots on three soil types. Over four years, the seed mixes produced similar amounts of biomass (8.27 ± 0.65 to 7.46 ± 0.65 Mg/ha). Seed mixes had relatively high yields compared to estimates from fertilized monocultures of perennial crops in the region. Species rich planting (16-32 species) may produce more biomass than less species rich plantings in years without flooding or drought. However, the effects of species richness on productivity are complicated by soil type. The mix with the highest species richness (32 species) had the lowest biomass production on the Waukee loam soil, but the highest biomass production on Spillville-Coland clay loam soil. Plantings with higher species richness were also less resistant to drought. However, species rich mixes (16 and 32 species) produced similar amounts of biomass compared to less species rich mixes (5 species) with the same dominant species. Finally, I found that increased species richness increased resistance to invasion by weeds and as few as five

species may provide high levels of resistance to invasion by weeds. The study suggests that the application of the BEF perspective of restoration may lead to weed resistant crops which are as productive, or more productive than low diversity crops.

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This Study by: Dustin R.J. Graham

Entitled: Biodiversity and Ecosystem Function and the Design
of Tallgrass Restorations For Biomass Production

has been approved as meeting the thesis requirement for the

Degree of Master of Science

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CHAPTER 1

INTRODUCTION

Recent interest in the use of diverse mixtures of plants as biomass feedstocks (Tilman et al. 2006a) has raised questions about the applicability of biodiversity and ecosystem function (BEF) research to ecological restoration. The Society for Ecological Restoration (SER; 2004) defines ecological restoration as “the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed.” Naeem (2006) breaks down the perspectives and goals of restoration into three categories: the community ecology perspective, the ecosystem function perspective and the Biodiversity-Ecosystem Function (BEF) perspective.

The community ecology perspective attempts to restore species and species persistence; biodiversity itself is often the goal of this perspective (Naeem 2006). The ecosystem function perspective is based on an ecosystem ecology view, being concerned with resource and energy and their movement in the system (Naeem 2006). Some distinguish ecosystem functions from ecosystem properties such as temporal stability, and the ability of a community to maintain function (resistance) or return to a similar level of a function (resilience) after perturbation (Naeem 2006). I will be using ecosystem function to include all these meanings. Finally, restoration from the BEF perspective alters abiotic conditions to achieve ecosystem function. Instead of viewing the community and ecosystem aspects of a system as separate, BEF research attempts to determine the separate influences of species richness, species function, and species interactions on ecosystem functions (Naeem 2006). Restorations from this perspective

attempt to achieve ecosystem function by restoring biodiversity. Naeem (2006) is careful to point out that the perspective which will be most effective will depend on the context and goals of the restoration. For example, many ecosystem functions in aquatic systems are more strongly affected by hydrology than biodiversity, and an ecosystem function perspective may be most appropriate.

Experiments have suggested that greater diversity may provide increased ecosystem function in many systems (Balvanera et al. 2006, Cardinale et al. 2007). However, the implications of BEF research for ecological restoration have been largely unexplored (Naeem 2006). Wright et al (2009) points out that only a few experiments have tested the BEF hypothesis in a restoration setting (Bullock et al. 2007, Bullock et al. 2001, Callaway et al. 2003). For example, Bullock et al. (2007) restored cereal crop fields with the goal of increased hay production and quality using a seven species grass mix, a government recommended grassland planting, and a 39-species mix of grasses and forbs which was designed to resemble local reference communities. Except for the first year after planting, the more species rich plots had higher productivity in all years examined (Bullock et al. 2001, Bullock et al. 2007). This study represents the application of the BEF perspective of restoration for three reasons. Seed mixes in the study resemble commonly used seed mixes for the site being studied; the ecosystem functions being examined are set by the goals of the restoration rather than arbitrary functions selected by the researcher; and seeding rates and plot maintenance reflect practical large-scale plantings as opposed to high seeding rates and hand-weeding of plots in some BEF research (Tilman et al 2006b).

The BEF perspective may be the most appropriate for the design of tallgrass plantings as sustainable replacements for fossil fuels (Tilman et al 2006a). A diverse mix of tallgrass species may supply important ecosystem functions for energy crops, specifically, high biomass productivity, low rates of invasion by weeds, and resistance to disturbance. Additionally, high diversity plantings may be multifunctional, providing additional benefits beyond these three specific goals. Compared to row crops, diverse perennial crops may have positive impacts on soil quality, water quality and wildlife populations (Robertson et al. 2008, Blanco-Canqui 2010, Meehan et al. 2010, Myers et al. 2011).

While the need for crops to supply biomass as a feedstock to replace oil consumption is growing (DOE 2005, DOE 2011, EPA 2010, EPA 2013), it is unclear how well BEF theory can currently inform the design of species rich plantings for biomass feedstocks. In this study, I attempt to apply a BEF perspective of ecological restoration to the design of tallgrass prairie plantings for use as low input biomass crops.

Biodiversity and Productivity

A number of experiments suggest increasing biodiversity leads to increased biomass productivity (Cardinale et al 2007; Balvanera et al 2006). These experiments explore the effect of biodiversity on ecosystem functions by growing a number of species in monoculture and comparing them with mixed species plots. Each species mixture is created by randomly selecting species from a pool of species grown in monocultures. This is done for a number of levels of species richness. Biomass productivity, pest

resistance and other ecosystem services provided by biodiversity are measured over time. Two long-term experiments which used these methods are the Biodiversity II experiment at the Cedar Creek Ecosystem Science Reserve, Minnesota, and the BIODDEPTH experiment in Europe (Tilman et al. 2006a, Hector et al 1999).

In the Biodiversity II experiment, Tilman et al. (2006a) established 168 plots containing 1, 4, 8 or 16 species on sandy, nitrogen-poor soil at the Cedar Creek Ecosystem Science Reserve. Species included in mixes were randomly selected from a pool of 18 native perennials. These mixes were seeded at a rate of 10 g/m² in 9m X 9m plots that were burned annually (Tilman et al. 2006b). After ten years, the study showed energy production from biomass increased with increasing species richness (Tilman et al. 2006a). After observing the effects of biodiversity on productivity, Tilman et al. (2006a) calculated that diverse tallgrass restorations on marginal farmland could potentially produce 1.5 times more energy than corn grain ethanol from corn grown on fertile soil.

The BIODDEPTH experiment used methods similar to the biodiversity II experiment, but was replicated at eight sites in seven European countries using 2x 2m or 2x5 m plots (Spehn et al. 2005). Overall, a log-linear relationship was found between above-ground biomass productivity and species richness; doubling the number of species increased productivity by 80 g/m² (Hector et al. 1999). Additionally, productivity increased linearly with an increased number of functional groups represented in the species mix. More specifically, the addition of a functional group increased yield by 100 g/m² (Hector et al. 1999).

A meta-analysis of BEF experiments by Cardinale and others (2007) found that diverse mixtures tended to produce more biomass than the average of all component species in monocultures (i.e., overyielding), but rarely produced more biomass than the single most productive monoculture of a component species (i.e., transgressive overyielding). In the 44 studies analyzed by Cardinale and colleagues (2007), diverse communities produced 1.7 times more biomass than the average of monocultures of all component species. By contrast, transgressive overyielding was only reported in 35% of mixtures which produced, on average, 12 percent less biomass than the most productive monoculture of any component species. This may seem discouraging for proponents of diverse bioenergy crops because it suggests that the most productive monocultures would be the most productive crops. However, diverse communities were more likely to show transgressive overyielding as time progressed (Cardinale et al. 2007). Therefore diverse plantings may outperform single species when average productivity is considered over time.

Biodiversity and Resistance to Disturbance

Greater diversity may also increase the stability of biomass productivity in a community. The insurance hypothesis predicts that in more diverse communities there is a higher chance that species will respond differently to environmental variation (Yachi and Loreau 1999). With some species responding positively and others negatively to any environmental variation, increasing diversity should dampen the effect of any disturbance (Tilman 1996; Yachi and Loreau 1999).

The first implication of this hypothesis is that diverse communities should have lower variation in productivity over time compared to less diverse communities. Hooper and colleague's qualitative review (2005) of experiments supported the lower long-term variability in diverse communities. Long running grassland experiments also suggest that diverse communities have lower variability in function over time (Caldeira et al. 2005, Tilman, Reich and Knops 2006).

Another implication of the insurance hypothesis is that diverse communities should have higher resistance to any single disturbance. Resistance compares the stock and rates of a community from pre-disturbance to disturbance conditions (Griffin et al 2009). For example, diverse plots were more resistant to drought than less diverse plots in grassland plots which differed in diversity due to nutrient gradients (Tilman and Downing 1994). When using tallgrass restorations to provide biomass feedstocks, resistance to disturbance may lead to a more consistent yields, decreasing the financial risk involved with growing such crops.

However, results of experiments examining the effect of diversity on stability are mixed. In a meta-analysis which examined 446 measurements of biodiversity and ecosystem function, Balvanera and colleagues (2006) found that the effect of biodiversity depends on the identity and intensity of the environmental variation. While biodiversity provided stability with variations in nutrients, biodiversity had no effect or negative effects with drought, temperature treatments, or with high levels of environmental variation. For example, Pfisterer and others (2004) experimentally induced drought in plots of the Swiss site of the BIODEPTH experiment. They found larger impacts of

drought on species rich grasslands than on lower diversity planting. While theory suggests that greater diversity will lead to more stable biomass productivity as the environment varies, the type and intensity of disturbance may be major factors in the stability of diverse communities.

Biodiversity and Resistance to Invasion

Many experiments have found that species-rich plantings are more resistant to invasion by weeds than less diverse plantings (Hooper et al. 2005 and Balvanera et al 2006). The mechanisms which cause species-rich communities to be more resistant to invasion include occupied functional space (Hooper and Duke 2010, Symstad 2000), a lower amount of light reaching the ground, and reduced availability of soil nutrients (Knops et al. 1999). Invasion decreases with increasing species richness as less resources are available for invading species to utilize.

Resistance to invasion is especially beneficial in diverse mixtures because the establishment of non-native and weedy species may undermine the positive effects of species richness on productivity. Invasion by non-natives may disrupt the complementary effects of native biodiversity thereby reducing productivity (Pfisterer et al. 2004). While increasing native diversity in a planting tends to increase productivity, increasing non-native diversity in plantings may not (Isbell and Wilsey 2011).

The suppression of weeds using herbicides is a common agricultural expense. BEF research suggests that the cost of weed suppression may be greatly reduced in diverse mixtures of native plants. The application of BEF theory to low input feedstocks

predicts that weeds will be less abundant in species rich plantings, reducing the maintenance cost of such crops.

The Relationship of Biodiversity to Ecosystem Function

The research described above indicates that species rich plantings will be productive, resistant to disturbance, and have low rates of invasion by weeds. However, these experiments also suggest that the effect of increasing biodiversity may level off with increasing species richness. In fact, most of the benefits of diversity may be present with relatively low species richness. In the BIODDEPTH experiment, Hector and Bagchi (2007) pointed out that only 8 to 16 species were needed to achieve similar levels of eight ecosystem functions compared to more diverse plantings. Hooper and colleague's review (2005) found that high levels of most ecosystem functions were achieved with five to ten species, but high levels of some functions were attained with as few as two species. Hector and colleagues (1999) found a log linear relationship between species richness and biomass productivity when analyzing results from eight sites across Europe, with a doubling of species needed for a certain amount of increase of the function in question. Evidence suggests that increasing biodiversity increases ecosystem function, but the amount of diversity required to achieve high levels of function may depend on the function being measured.

The relationship of biodiversity to ecosystem function may also be context-dependent. In the BIODDEPTH experiment, the BEF relationship was found to be log-linear, when considering all seven countries together. However, when field sites were

considered individually, three sites had no detectable relationship between species richness and biomass production, while two sites had linear relationships, with each additional species in a mixture making similar contributions to ecosystem functioning (Hector et al. 1999). In their meta-analysis, Balvanera and others (2006) also found the location of a study had a strong influence on the result of the BEF experiment. While a general trend that increasing biodiversity leads to increased ecosystem function is clear, the relationship may be dependent on variables associated with location.

In situations where a BEF perspective of restoration is appropriate, restoration goals for certain ecosystem functions may be met with relatively few species compared to the species richness of remnant communities, as the known benefits of species richness typically begin to reach saturation at relatively low species richness (Hector and Bagchi 2007, Cardinale et al. 2006). However, the BEF relationship may vary at smaller spatial scales (Hector et al. 1999). Additionally, with little evidence to suggest precisely how much species richness is needed to attain an adequate level of the function or functions needed to meet restoration goals, BEF theory remains only a general guiding concept rather than a semi-predictive tool (Naeem 2006). Detailed studies of the application of the BEF perspective of restoration are lacking, but are needed to test BEF theory and to inform the practice of ecological restoration (Naeem 2006).

The Application of BEF to Restoration

The random selection of species from species pools in BEF experiments allows researchers to apply their findings to the general function of biodiversity. Experiments that use these methods suggest that species rich tallgrass plantings could be productive crops with more resistance to disturbance and invasion by weeds than less diverse plantings. However, experiments like those described above have been criticized, as it is unclear how well random species assemblages reflect natural communities. Exploring all possible combinations of species in a BEF experiment may not resemble the way communities are assembled and species are lost in natural communities (Hooper 2005, Weiher and Keddy 1999). This criticism also applies to plantings in which seed mixes are designed as in most applications of the BEF perspective of restoration. These designed mixes are typically not random selections of local species. Rather, they reflect reference communities or seed mixes from previously successful restorations (Smith et al. 2010, Bullock et al 2007). While results from the BEF experiments described above may apply to restorations, well recorded applications of the BEF perspective of restoration are rare (Wright et al 2009, Naeem 2006), and such experiments are needed to test BEF theory and inform ecological restoration.

In this study, I examine the effectiveness of the BEF perspective of restoration in the design of native tallgrass plantings as biomass crops. The ecosystem functions that I measure are those that are important for the use of the plantings as biomass crops. Seed mixes were designed rather than randomly constructed. Additionally large scale (0.33 to 0.55 ha) plots were used, seeding rates were typical of native plantings in the region

(Smith et al. 2010), and plots were not hand weeded. Using these methods, this experiment tests the application of BEF theory in a restoration setting. Specifically, I test whether planting tallgrass prairie restorations with seed mixes which vary in species richness affects some ecosystem functions which are important for the success of tallgrass prairie plantings as biofuel feedstocks. I compare biomass productivity (Mg/ha of biomass), resistance to invasion by weeds (g/m² of weed biomass), and resistance to drought (absolute change, Mg/ha, in biomass from pre to drought conditions) of four designed seed mixes which range in species richness. Based on the experiments reviewed above, I predict that more species-rich plantings will have higher levels of these three ecosystem functions.

CHAPTER 2

METHODS

Site Description

In 2008, the Tallgrass Prairie Center (TPC) of the University of Northern Iowa established a biomass research site on a portion of the Cedar River Natural Resource Area (CRNRA) south of Waterloo, IA (N 42.3861, W -92.22241). The TPC rented the study site from the Black Hawk County Conservation Board, which acquired the property in 1973. Since purchasing the area, the conservation board had leased the fields of the study site for corn and soybean production. The fields at CRNRA are separated by wooded fencerows consisting largely of Siberian elm (*Ulmus pumila*). At a larger scale, the site is near the Cedar River and surrounded by riparian woodland and row-crops (Figure 1). The mean of daily mean temperature from 1980 to 2010 at the site was 8.8⁰ C (SD= 0.81) and the 30 year mean annual precipitation was 87.0 cm (SD=18.14, NOAA 2014).

The configuration of soils at CRNRA allowed me to test the productivity and weed resistance of tallgrass prairie plantings over three soil types that vary in drainage and fertility (Table 1, Figure 1). All three soils are relatively flat with 0-2% slope. 1) The excessively drained, Flagler sandy loam soil has a Corn Suitability Rating (CSR) of 55 and sandy composition, 64.6% sand, 14.8% clay, and 20.6% silt (NRCS 2014). 2) The well-drained Waukee loam soil has a CSR of 72 and is composed of 38.5% sand, 21.7% clay, and 39.8% silt (NRCS 2014). 3) The Spillville-Coland alluvial complex is a poorly drained soil with a weighted average composition of 29.5% sand, 26.3% clay and 44.2% silt with an average CSR of 74 (NRCS 2014). Before planting the seed mixes, the surface

soil was measured for soil organic carbon, total nitrogen, and carbon to nitrogen ratio (Table 1, Cambardella, personal communication, 2008). The above soils will be referred to respectively as sand, loam and clay.

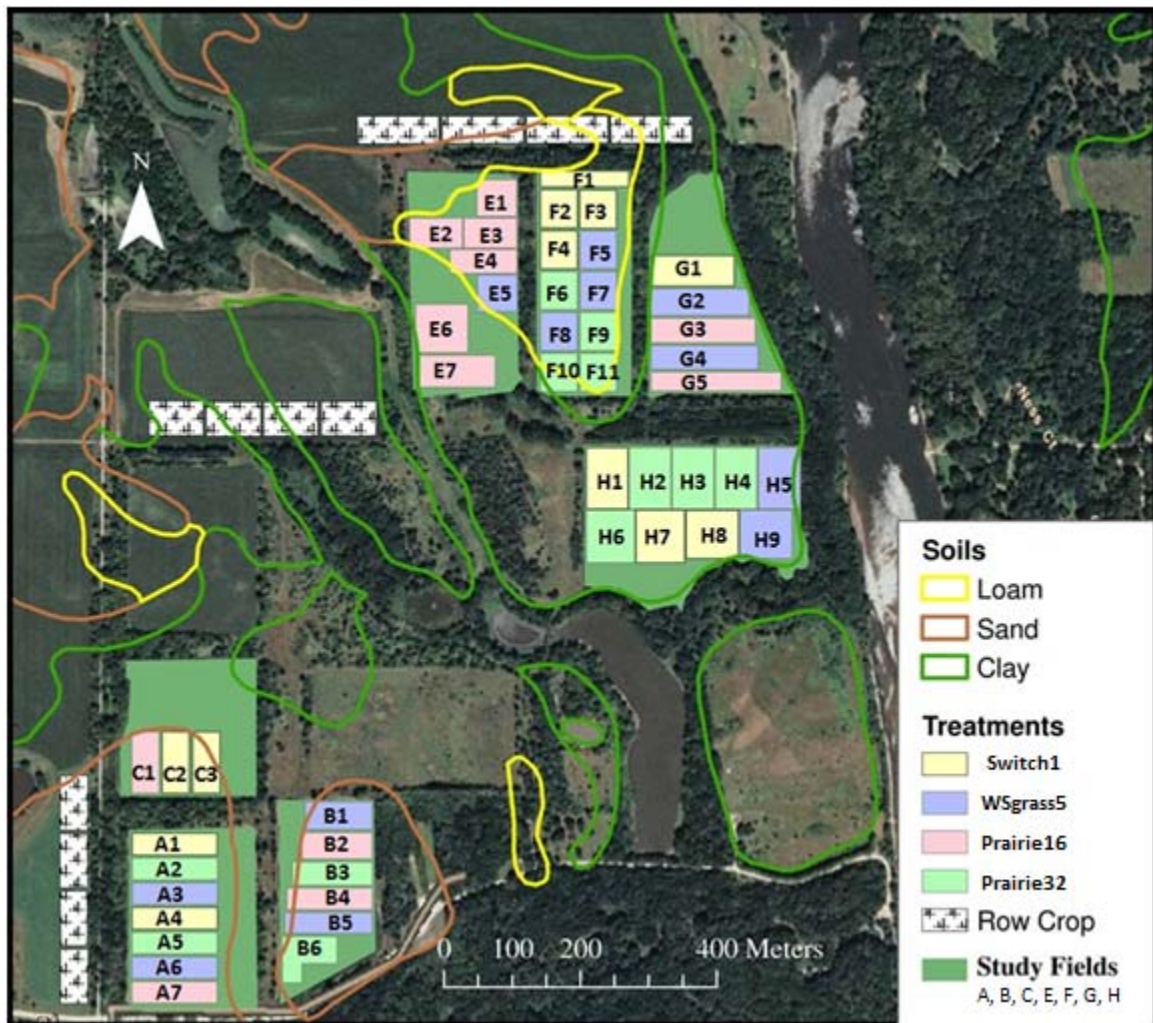


Figure 1: Map of CRNRA research area. Plot names, soils, and treatments are included. (With permission from Jim Mason)

Table 1: Soil characteristics of the three soils used in this study. Soil composition (silt, clay, and loam), corn suitability rating (CSR), Total Nitrogen (TN), Soil Organic Carbon (SOC), and Carbon to nitrogen ration (C/N). SOC and TN are mg/g. Composition and CSR from NRCS (2014). SOC, TN and C/N courtesy of Cynthia Cambardella (Personal communication, 2008).

SOIL TYPE	SAND	CLAY	SILT	CSR	TN	SOC	C/N
SAND	64.6%	14.8%	20.6%	55	1.44	14.24	9.88
LOAM	38.5%	21.7%	39.8%	72	2.14	23.37	10.93
CLAY	29.5%	26.3%	44.2%	74	2.29	24.9	10.86

Seed Mixes

Perennial, native seed mixes compared in this study were designed with four levels of species-richness. The seed mixes were: (1) Switch1: a monoculture of *Panicum virgatum*, (2) WSgrass5: a five species mix of carbon-4 photosynthesis (C4) grasses native to the tallgrass prairie, (3) Prairie16: a 16 species mix including C4 and carbon-3 photosynthesis (C3) grasses, legumes and non-leguminous forbs, and (4) Prairie32: a 32 species mix including C4 and C3 grasses, sedges, legumes and non-leguminous forbs. Seed mixes include the species from lower diversity treatments. For example, the prairie treatment contains all species from the biomass treatment plus 16 additional species. Mixes were seeded at 561 to 869 pure live seed per m² (Table 2). Species, functional group and seeding rate for each seed mix can be found in Table 2.

Table 2: Species, functional groups, and seeding rates of the four treatments used in this study (units are pure live seed per square meter).

Scientific	Common Name	Function	---Seeding Treatments---			
			Switch1	WSgrass5	Prairie16	Prairie32
<i>Panicum virgatum</i>	Switchgrass	C4 grass	561	86	43	32
<i>Bouteloua curtipendula</i>	Side-oats Grama	C4 grass	~	86	43	32
<i>Sorghastrum nutans</i>	Indian Grass	C4 grass	~	86	43	32
<i>Andropogon gerardii</i>	Big Bluestem	C4 grass	~	151	151	135
<i>Schizachyrium scoparium</i>	Little Bluestem	C4 grass	~	151	151	135
<i>Sporobolus compositus</i>	Tall Dropseed	C4 grass	~	~	~	32
<i>Elymus canadensis</i>	Canada Wildrye	C3 grass	~	~	43	32
<i>Elymus virginicus</i>	Virginia Wild Rye	C3 grass	~	~	43	32
<i>Agropyron smithii</i>	Western Wheatgrass	C3 grass	~	~	43	32
<i>Carex bicknellii</i>	Copper-shoulder oval sedge	C3 grass	~	~	~	32
<i>Carex brevior</i>	Plains oval sedge	C3 grass	~	~	~	32
<i>Carex grvida</i>	Heavy Sedge	C3 grass	~	~	~	32
<i>Astragalus canadensis</i>	Milk Vetch	Legume	~	~	38	16
<i>Desmodium canadense</i>	Showy Tick Trefoil	Legume	~	~	38	16
<i>Lespedeza capitata</i>	Round-Headed Bush Clover	Legume	~	~	38	16
<i>Amorpha canescens</i>	Leadplant	Legume	~	~	~	16
<i>Baptisia leucantha</i>	White Wild Indigo	Legume	~	~	~	1
<i>Dalea purpurea</i>	Purple Prairie Clover	Legume	~	~	~	16
<i>Silphium laciniatum</i>	Compass Plant	Forb	~	~	3	3
<i>Helianthus grosseserratus</i>	Saw-tooth Sunflower	Forb	~	~	38	16
<i>Helopsis helianthoides</i>	Ox-eye Sunflower	Forb	~	~	38	16
<i>Oligoneuron rigidum</i>	Stiff Goldenrod	Forb	~	~	38	16
<i>Ratibida pinnata</i>	Yellow Coneflower	Forb	~	~	38	16
<i>Artemisia ludoviciana</i>	Prairie Sage	Forb	~	~	~	16
<i>Echinacea pallida</i>	Pale Purple Coneflower	Forb	~	~	~	16
<i>Eryngium yuccifolium</i>	Rattlesnake Master	Forb	~	~	~	16
<i>Monarda fistulosa</i>	Wild Bergamot	Forb	~	~	~	16
<i>Phlox pilosa</i>	Prairie Phlox	Forb	~	~	~	3
<i>Symphyotrichum laeve</i>	Smooth Blue Aster	Forb	~	~	~	16
<i>S. novae-angliae</i>	New England Aster	Forb	~	~	~	16
<i>Tradescantia bracteata</i>	Prairie Spiderwort	Forb	~	~	~	16
<i>Zizia aurea</i>	Golden Alexanders	Forb	~	~	~	16

Total Seeds Sowed/M²

561 560 829 869

Perennial, native seed mixes were designed based on the following criteria. Since a monoculture of switchgrass has been recommended as a productive, perennial energy crop, it was included to compare with more diverse plantings. Native C4 grasses, especially big bluestem (*Andropogon gerardii*) and little bluestem (*Schizachyrium scoparium*), were observed to be very productive in previous research. As such, a mix of C4 grasses was designed. In addition to these five C4 grasses, the Prairie16 mix adds 11 species including cool-season grasses, forbs and legumes. Species selection for the biomass treatment was based on nine criteria. The selected plants were adapted to a wide range of habitats, widely distributed, easy to establish, long lived, vegetatively productive with readily available seed, biomass which would remain upright until spring, and the ability to coexist with other species. Various species exhibiting a range of phenologies were included in the seed mix (Appendix A). In addition to including the species from the Prairie16 mix, the Prairie32 mix was designed to resemble a diverse prairie planting in the region.

Design, Establishment, and Maintenance

Four replicates of each seed mix were randomly assigned to plots on each of three soil types for a total of 48 plots. Plots ranged from 0.33 to 0.55 ha (0.8 to 1.4 acres). All research plots were seeded in late May and early June of 2008, but shortly thereafter were inundated for more than two weeks by the Cedar River. Due to large scale scouring and siltation by the flood, it was necessary to replant the plots in 2009. In order to reduce weed pressure and insure that the previous planted seeds would not be present to influence the results of the study, the fields were planted with glyphosate resistant

soybeans (*Glycine max*) after the flood had receded in July of 2008. Glyphosate was applied in July and August to control weed pressure and eliminate any effect of the 2008 planting.

The site was reseeded in spring 2009. Seed was drilled directly into soy bean stubble between May 25 and June 5, 2009. Plots were planted from the least diverse mix to most diverse mix using a Truax native seed drill. The drill boxes were cleaned between planting of the seed mixes. Establishment mowing was conducted on June 26, 2009. While many plantings require multiple mowing during the first growing year, the site had lower than typical weed establishment during the first growing season (see Smith et al. 2010, for establishment mowing guidelines). The presence of less weeds was likely due to the limited disturbance from drilling into stubble and years of chemical weed suppression on the site.

Non-plot areas were planted in fall 2008 with a mix similar to the prairie treatment but at double the seeding rate (Figure 1). To limit the colonization of plants from one plot to another, a 2m wide strip was planted with a commercial pasture mix. This 2m wide lane around each plot was maintained by multiple mowings each growing season. Research plots were burned on April 5, 2011. Plot A7 (Figure 1) was hayed on November 12, 2011 to provide biomass for a pelletization test. All research and non-plot areas were hayed, except A7, from March 26 to March 30, 2012 to provide material for pelletization and conducting a test burn at Cedar Falls Utilities. In 2013, plots received no management.

Sampling Methods

Basal area for each species was annually estimated in each plot. Two, 10 m transects were randomly located in each plot, one running East to West, the other North to South. To avoid edge effects, no transect was placed within one meter of any plot edge. Ten 0.1m² quadrats (20cm X 50cm) were sampled at one meter intervals along the South or West side of the transect. Percent cover of each species was estimated at 2.5 cm above the ground. Presence of species not included in the seed mix for a plot were recorded. Basal area sampling was conducted from June 17 to 24, 2010; July 8 to July 22, 2011; July 16 to July 27, 2012 and July 8 to 19, 2013.

Above-ground biomass was measured by clipping plants at ground level, sorting plant material by functional group, drying plant biomass at 65°C for 72 hours, and weighing the dried plant biomass in each functional group. Dead material on the ground was excluded from the sample, but standing dead material was included. The functional groups considered were C4 grasses, C3 grasses, legumes, non-leguminous forbs and weeds (Table 2). Any plant which was not included in the seed mix for a plot was included in the weeds functional group. The sampling protocol differed slightly in 2013 versus years 2010 – 2012. More specifically, in 2010-2012, 10 sub-samples were collected from randomly located 0.1m² quadrats. In 2013, quadrat size was increased to 0.3 m² to provide enough plant material for combustion analysis. Biomass samples were taken from August 25 to September 3 in 2010; August 29 through September 12, 2011; August 28 to Sept 13, 2012, and from Sept. 2 to Sept. 27, 2013. These dates reflect the time of peak biomass production of switchgrass in the region (Heaton et al 2004).

Statistical Analysis

The above-ground biomass of all functional groups including weeds and the weed biomass alone were compared using univariate repeated measure ANOVAs with years as the repeated measure and seed mix and soil type as factors. Univariate repeated measures ANOVA is appropriate when the same trait is measured multiple times on the same subject, plots in my case (SYSTAT 2009). The assumptions of repeated measures ANOVA include normality and compound symmetry, which includes the homogeneity of variances and the similarity of the covariance of all pairs of repeated measures (SYSTAT 2009).

I evaluated normality within cells with the Anderson-Darling test and evaluated the assumption of compound symmetry with the Huynh-Feldt ϵ statistic using the corresponding correction to p-values when appropriate (SYSTAT 2009). Total biomass data was normal ($p > 0.15$), and met the assumption of compound symmetry ($\epsilon = 1.00$). Weed biomass was log+1 transformed to meet the assumption of normality, even after the log+1 transformation the WSgrass5 and Prairie16 on the sand soil in 2013 violated normality. The log+1 transformation was retained since violations were minor. After the log +1 transformation the weed data also met the assumption of compound symmetry ($\epsilon = 1.00$).

Post-hoc tests for repeated measures are complex and methods for calculating confidence intervals and inference tests have only recently been developed (Lofus and Mason, 1994; Jarmasz and Hollands, 2009; Hollands and Jarmasz 2010). Since more data about the variability of a cell is available with repeated measures than is available in

ANOVA models without repeated measures, it is beneficial to retain this information when creating confidence intervals and when conducting post hoc comparisons (Lofus and Mason, 1994). For each repeated measures ANOVA, confidence intervals were calculated following Jarmasz and Hollands (2009) using MS of the error term from the repeated measure ANOVA as an estimate of variability. Post-hoc tests follow Lofus and Mason (1994) by multiplying the 95% confidence intervals by $\sqrt{2}$ and comparing this to the difference in means between pairs. In results “n” represents trials (measurements of plots) and “N” represents subjects (plots).

I explored the resistance of seed mixes to disturbance by drought by calculating the difference in mean biomass production of each plot between 2011, a relatively normal year, and 2012, a drought year. The absolute difference in biomass production was compared using a two-way ANOVA with soils and treatments as factors. Data met the assumptions of normality (Shapiro-Wilk $p = 0.90$) and homoskedastiaty (Levene’s test $p=0.952$). Soil and the two-way interaction were not significant, and the model with the lowest Akaike Information Criteria was used, which included only the seed mix term. A Fisher’s LSD test was used for post-hoc comparisons of seed mixes. Repeated measures ANOVA for total biomass production was conducted in Minitab 16. All other statistics were computed using Systat 13 except for those in Appendix B which were conducted in PRIMER 6. All Graphs were created using SigmaPlot 10, except for Appendix B which was created in PRIMER 6.

CHAPTER 3

RESULTS

Yearly Temperature, Precipitation, and Flooding

The average growing season (February to September) precipitation from 2010 to 2013 was 82.63 cm, slightly higher than the thirty year average for the area of 75.63 cm (SD = 18.00, NOAA 2014). The annual growing season precipitation for 2010 to 2013 was 97.36 cm in 2010, 59.54 cm in 2011, 40.46 cm in 2012, and 87.73 cm in 2013 (NOAA 2014). I will be using the term drought to refer to 2012 since that year had precipitation that was 1.95 standard deviations lower than the 30 year mean growing precipitation for the site. Although above average rainfall occurred in the summer of 2010, the site did not flood. On May 31, 2013, the Cedar River adjacent to the research site had it's 12th highest flood crest on record (NWS 2014). The research site flooded, with water remaining over the clay soil from May 24 to June 30. The loam was inundated in the first week of June, with less than 30 cm of water (Myers and Hokschi, personal communication, 2013). The sandy soil did not flood in 2013 (Myers and Hokschi, personal communication, 2013). I will be referring to the events of 2013 as disturbance by flooding.

The timing of precipitation also varied with an especially wet summer in 2010, a wet spring in 2013 and dry summers in 2011, 2012, and 2013 (NOAA 2014, Figure 2). The 30-year average temperature for the growing season at the site was 13.2⁰ C (NOAA 2014). Except for 2013, most years of the study had above average temperatures (NOAA 2014, Figure 3).

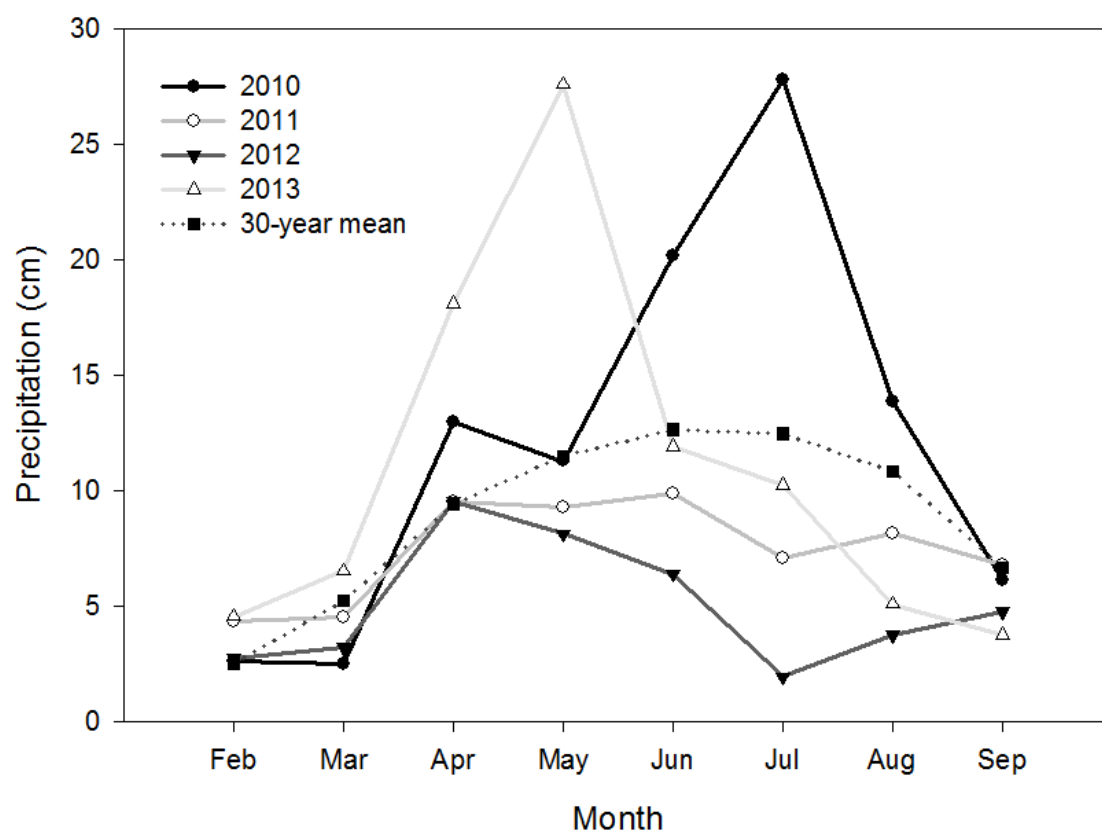


Figure 2: Monthly precipitation from 2009 to 2013 and 30 year average. Data was recorded by the Waterloo Airport weather station, 16 miles northwest of the research site (NOAA 2014).

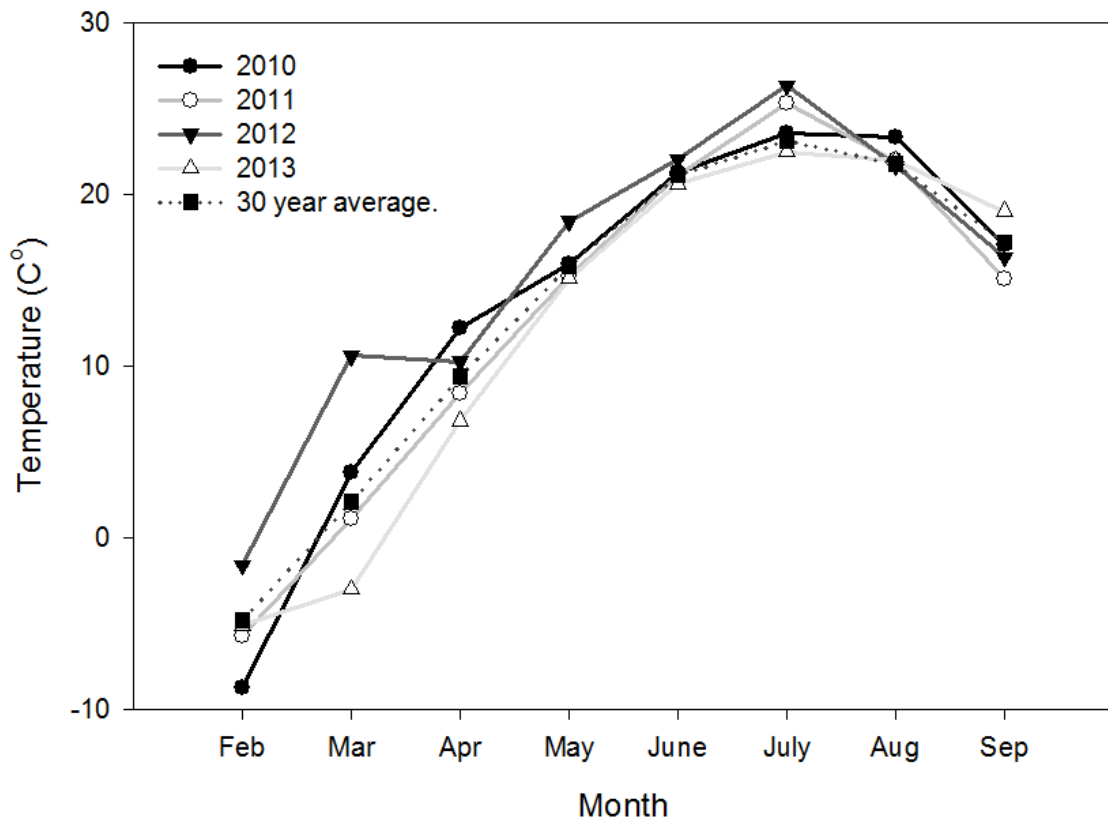


Figure 3: Monthly temperature (from daily average temperature) for 2010 to 2013 with the 30-year average recorded by the Waterloo Airport weather station, 16 miles northwest of the research site (NOAA 2014).

Biomass Yield

The average biomass yield (total of all functional groups including weeds) of all plots over the four years was 8.06 Mg/ha. Mean Biomass productivity and ranged from 3.42 Mg/ha, the WSgrass5 on sand in 2012, to 14.57 Mg/ha, the Prairie16 on clay in 2011 (Appendix E). Over the three soils and four years, no significant difference in biomass yield was detected between seed mixes ($p = 0.266$, Table 3). Over the three soils and four

years, Switch1 had the highest mean biomass yield with 8.274 ± 0.647 Mg/ha, followed by the Prairie16 mix with 8.257 ± 0.6427 Mg/ha, the Prairie32 mix with 8.227 ± 0.647 Mg/ha, and the WSgrass5 with 7.492 ± 0.647 Mg/ha. However, seed mixes responded differently to soils ($p < 0.028$) and years ($p < 0.017$, Table 3).

Table 3: Repeated measures ANOVA table for total biomass yield (Mg/ha) from 2010 to 2013. Comparing mean biomass production of all functional groups sampled including weed biomass (n=192, N=48).

Between Subjects	SS	df	MS	F-Ratio	p-Value
Soil	171.471	2	85.735	17.592	<0.001
Seed Mix	20.864	3	6.955	1.427	0.251
Soil*Seed Mix	79.516	6	13.253	2.719	0.028
BS error	175.448	36	4.874		
Within Subjects	SS	df	MS	F-Ratio	p-Value
Year	736.597	3	245.532	55.719	<0.001
Year*Soil	157.096	6	26.183	5.942	<0.001
Year*Seed Mix	94.298	9	10.478	2.378	0.017
Year*Soil*Seed Mix	50.28	18	2.793	0.634	0.824
WS error	475.911	108	4.407		

Biomass yields differed between seed mixes within each year of the study. In 2010, Prairie32 produced 24.3% more biomass than Switch1 (Figure 4, Table 4). In 2011, Prairie16 produced 16.1% more biomass than Switch1 and 27.3% more than WSgrass5 (Figure 4, Table 4). In 2011, Prairie32 produced 16.0% more biomass than Switch1 and 27.2% more than WSgrass5. In 2012, the Switch1 produced 20.8% more biomass than WSgrass5, 19.1% more than Prairie16, and 23.0% more than Prairie32 (Figure 4, Table 4). In 2013, the Switch1 produced 22.3% more biomass than WSgrass5, 17.7% more than Prairie16, and 26.0% more than Prairie32 (Figure 4, Table 4).

Over the four years, the Prairie32 mix was more productive than the WSgrass5 and Prairie16 on the loam soil (Figure 5, Table 5). However, the Prairie32 mix produced significantly less biomass than the Prairie16 mix on the clay soil (Figure 5, Table 5). Throughout the study, all four mixes produced similar amounts of biomass on the sand soil (Figure 5, Table 5).

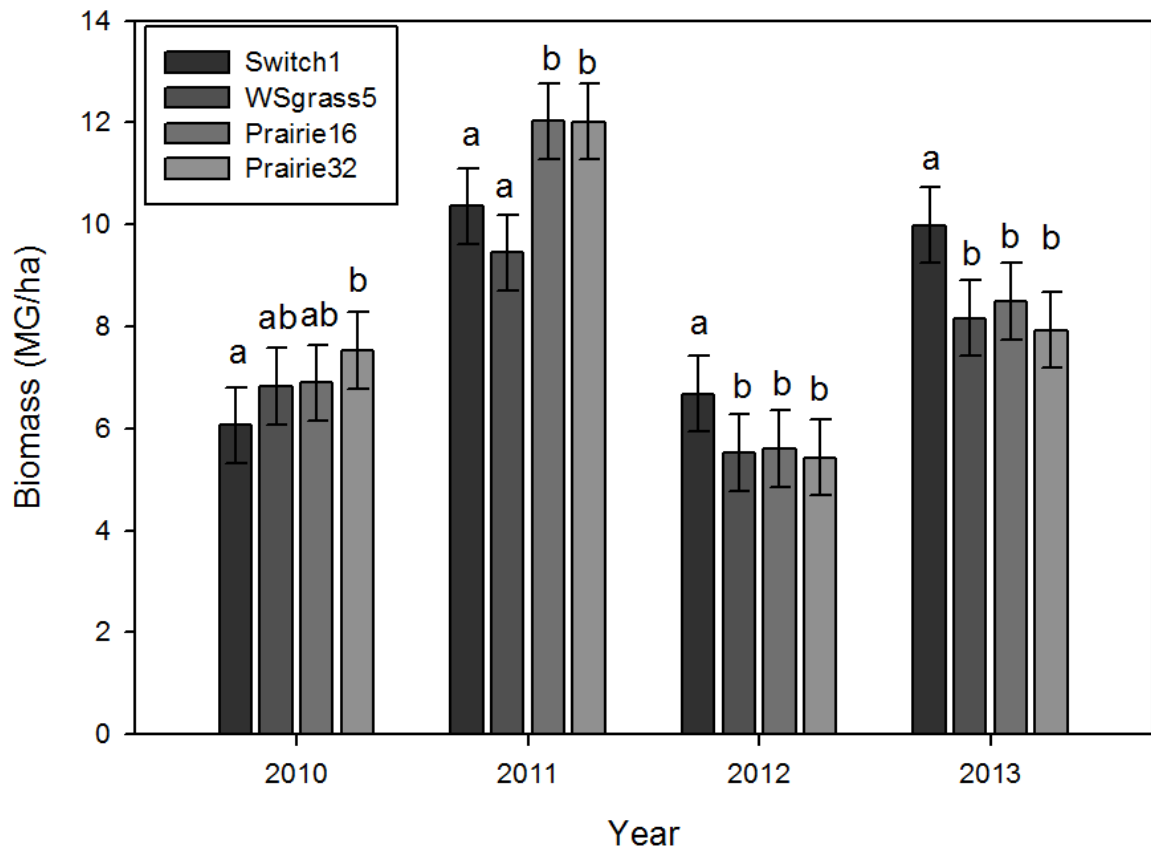


Figure 4: Mean yield (Mg/ha) of the four seed mixes for each year of the study averaged over soils, with 95 % confidence intervals (n = 48, N=12). Letters represent significant differences between seed mixes within years.

Table 4: Mean yield (Mg/ha) of seed mixes for each year of the study averaged over soils (n = 48, N=12). Significant differences were determined using Least Significant Difference (LSD) following Hollands and Jarmaz (2010) and Lofus and Mason (1994). Letters represent significant differences between seed mixes within years.

	Switch1	WSgrass5	Prairie16	Prairie32	LSD
2010	6.06 ^a	6.83 ^{ab}	6.90 ^{ab}	7.53 ^b	1.06
2011	10.36 ^a	9.45 ^a	12.03 ^b	12.02 ^b	1.06
2012	6.68 ^a	5.53 ^b	5.61 ^b	5.43 ^b	1.06
2013	9.99 ^a	8.17 ^b	8.49 ^b	7.93 ^b	1.06

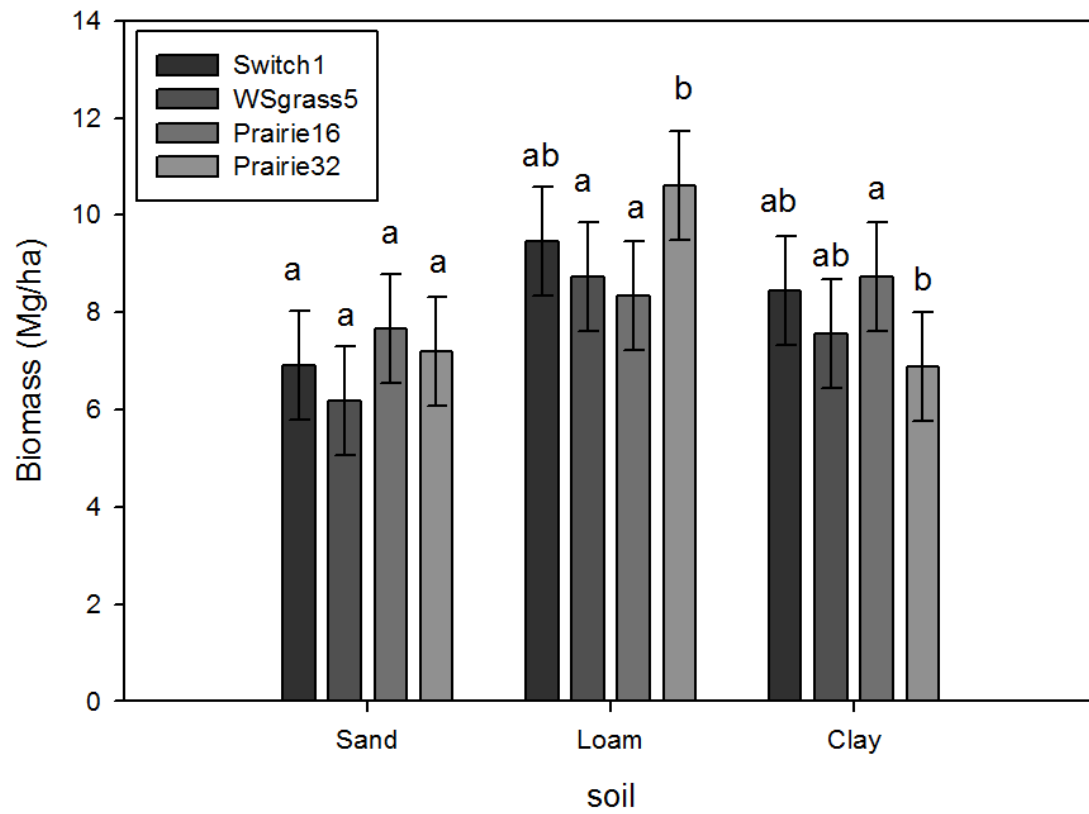


Figure 5: Mean yield (Mg/ha) of the four seed mixes for each soil averaged over the four years with 95% confidence intervals (n=16, N=4). Letters represent significant differences between seed mixes within soil types.

Table 5: Seed mix means (MG/ha) and pair-wise significance of seed mix for each soil averaged over the four years (n=16, N=4). Significant differences were determined using Least Significant Difference (LSD) following Hollands and Jarmasz (2010) and Lofus and Mason (1994). Letters represent significant differences between seed mixes within soils.

	Switch1	WSgrass5	Prairie16	Prairie32	LSD
Loam	9.46 ^{ab}	8.74 ^a	8.36 ^a	10.61 ^b	1.58
Clay	8.44 ^{ab}	7.56 ^{ab}	8.74 ^a	6.88 ^b	1.58
Sand	6.92 ^a	6.18 ^a	7.68 ^a	7.20 ^a	1.58

Drought Effects on Biomass Yield

The drought in 2012 decreased biomass production in all seed mixes. From 2011 to 2012 biomass production decreased by 36% in Switch1, 42% in WSgrass5, 55% percent in Prairie16, and 54% in Prairie32. The absolute decline in biomass production differed by seed mixes ($p = 0.044$, Table 6). Prairie16 and Prairie32 had significantly larger declines in absolute biomass production than Switch1 and WSgrass5 seed mixes (Figure 6).

Table 6: ANOVA comparing the decrease in biomass production (Mg/ha) from 2011, a relatively average year, to 2012, a drought year (N= 48). The soil factor and the seed mix by soil interaction were not significant and were removed, improving the model.

Source	Type III SS	df	Mean Squares	F-Ratio	p-Value
Seed Mix	88.507	3	29.502	2.935	0.044
Error	442.333	44	10.053		

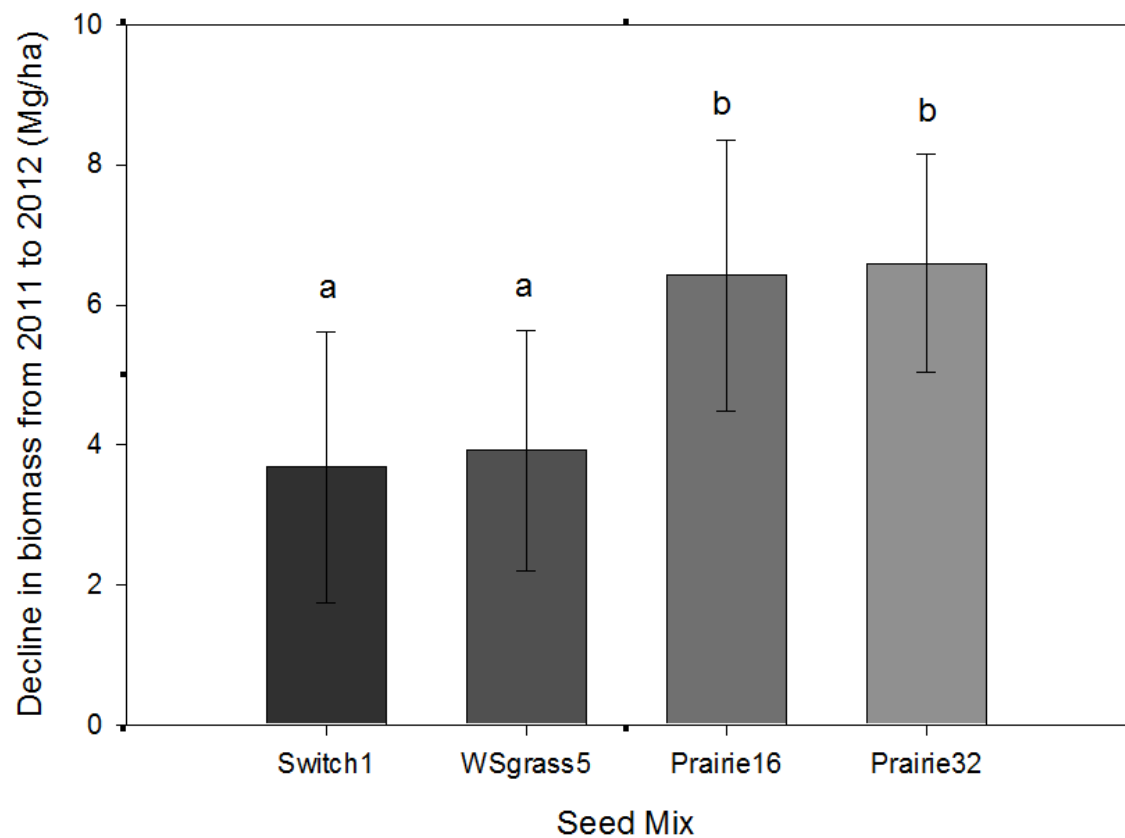


Figure 6: The decline in biomass production (Mg/ha) between four seed mixes from 2011 to 2012 (N=12). Error bars are 95% confidence intervals from standard deviation. Letters represent significantly different groups based on Tukey's test.

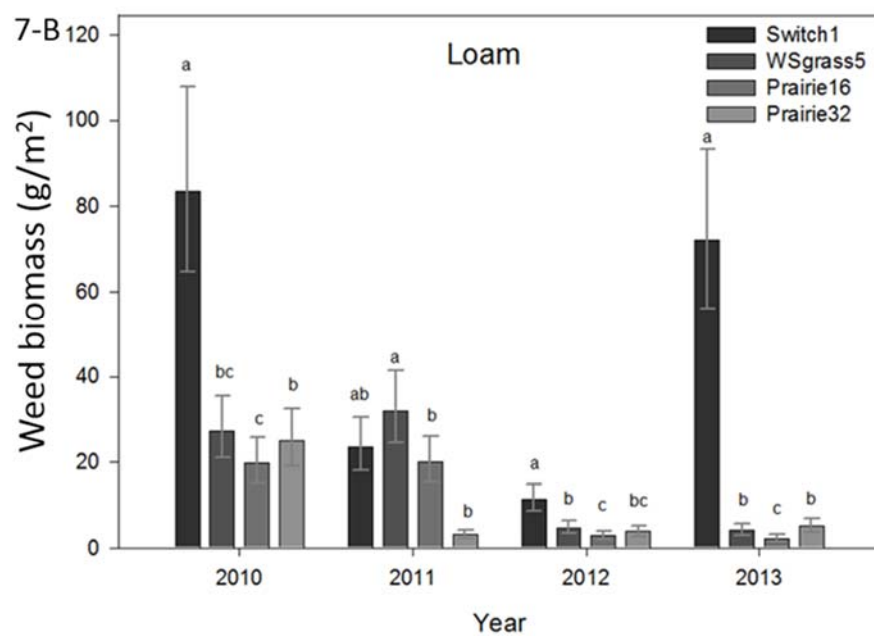
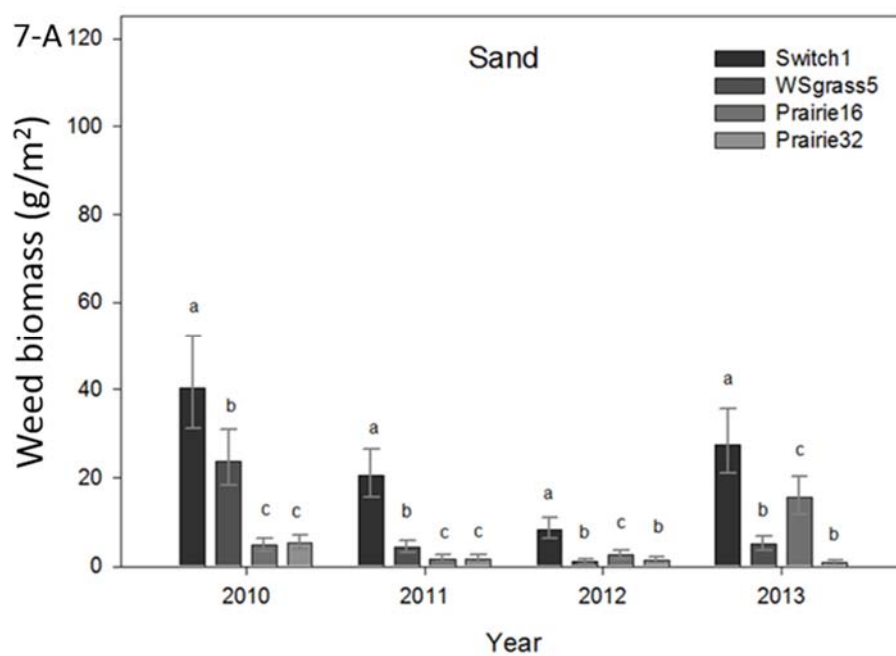
Weed Biomass

Averaging over the four years, the percentage of weed biomass to total biomass in the seed mixes was 6.1% in Switch1, 2.9% in WSgrass5, 2.3% in Prairie16, and 1.8% in Prairie32. Over four years, switchgrass monocultures had significantly more weed biomass than all other seed mixes (Table 7, Figure 7, Table 8). In all seed mixes, weed biomass decreased significantly each year until 2013, with a large drop in 2012 (Figure 8, Table 9).

Weed biomass responded differently to combinations of seed mixes, soils and years ($p < 0.001$, Table 7). Switch1 had significantly higher weed biomass than the other three seed mixes on most soils in most years (Figure 7). However, Switch1 was not significantly different than other mixes on loam soil in 2011 (Figure 7-B). On clay soil, Switch1 had lower weed biomass than WSgrass5 in 2010, and lower weed biomass than Prairie 16 in 2013.

Table 7: Repeated Measures ANOVA table for weed biomass (g/m^2) from 2010 to 2013. Data were log+1 transformed before analysis (n=192, N=48).

Between Subjects	SS	df	MS	F-Ratio	p-Value
Soil	4.930	3	2.465	7.458	<0.001
Seed Mix	13.775	2	4.592	13.892	0.002
Soil*Seed Mix	0.648	6	0.108	0.327	0.919
BS error	11.899	36	0.331		
Within Subjects	SS	df	MS	F-Ratio	p-Value
Year	8.192	3	2.731	16.829	<0.001
Year*Soil	1.825	9	0.304	1.875	0.004
Year*Seed Mix	4.221	6	0.469	2.890	0.092
Year*Soil*Seed Mix	8.720	18	0.484	2.986	<0.001
WS error	17.524	108	0.162		



(figure continues)

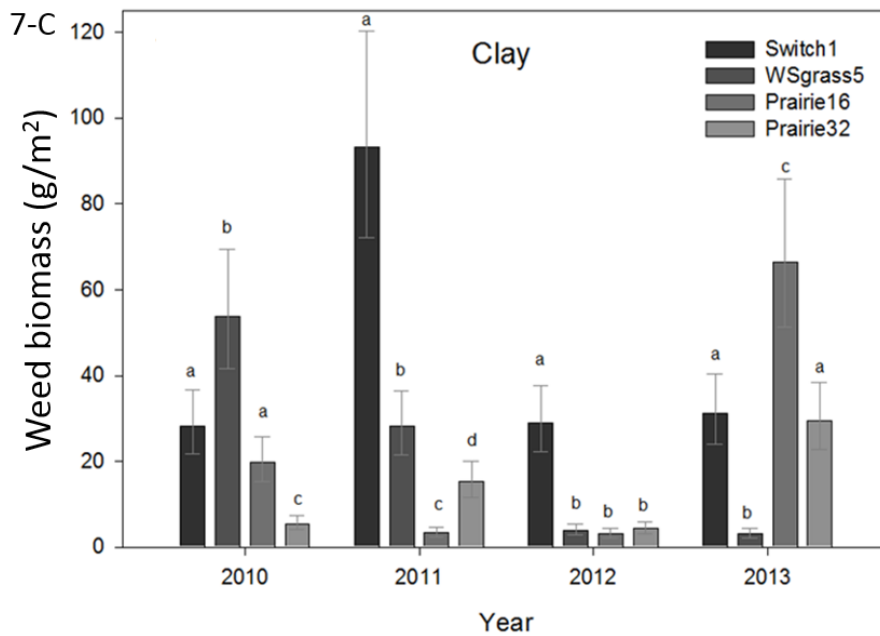


Figure 7: Weed biomass by seedmix, soil and year. Back-transformed (geometric) means of weed biomass of seed mixes by year (g/m²) with 95 % confidence intervals for A) Sand B) Loam and C) Clay soils (n = 16, N = 4). Letters represent significant differences between seed mixes within years based on LSD following Hollands and Jarmasz (2010) and Lofus and Mason (1994).

Table 8: Weed biomass by seed mix. Back-transformed (geometric) means, means of log+1 transformed data (Mg/ha), and LSD value for the log mean (n=48, N=12). Letters represent significant differences (LSD = 0.198).

	Switch1	WSgrass5	Prairie16	Prairie32
Geometric mean	32.36	10.47	8.13	6.46
Log +1 mean	1.51 ^a	1.02 ^b	0.91 ^b	0.81 ^c

Table 9: Weed biomass(Mg/ha) by year. Back-transformed (geometric) means, means of log+1 transformed data, and LSD value for the log means (n=48, N=12). Letters represent significant differences (LSD = 0.239).

	2010	2011	2012	2013
Geometric mean	20.99	12.27	5.55	12.25
Log +1 mean	1.322 ^a	1.089 ^b	0.744 ^c	1.088 ^b
LSD	0.081	0.081	0.081	0.081

CHAPTER 4

DISCUSSION

Biomass Productivity

Biodiversity and ecosystem function research suggests that, over time, low input species rich plantings would produce more biomass than plantings with few species (Tilman et al. 2006a, Hooper et al. 2005, Cardinale et al. 2007, Balvanera et al. 2006). I found that over four years, biomass yields were similar between seed mixes. In fact, there was only a 0.5% difference in the four year mean biomass production between the least and most diverse mixes. However, biomass production of the seed mixes was affected differently by soil and by years.

Diverse mixes may be more productive than mixes with few species in years without disturbance by drought or flooding. Prairie16 and Prairie32 produced more biomass in the early years of the study, 2010 and 2011, while Switch1 produced more biomass than all other mixes in the last two years of the study, 2012 and 2013. Annual differences in biomass production were likely caused by environmental variation. Prairie16 and Prairie32 had higher yields than other seed mixes in 2010, a wet year without disturbance from flooding. The growing season precipitation in 2011 was the most similar to the thirty year average and Prairie16 and Prairie32 produced more biomass than Switch1 or WSgrass5. In 2012 drought may have affected the productivity of Prairie16 and Prairie32 more strongly than that of Switch1 or WSgrass5. Switch1 produced the highest yields in 2013 with disturbance by flooding on two of the three soil types. If 2010 and 2011 reflect the relationship of planted species richness to biomass

productivity in years without disturbance by drought or flooding, then my results support a positive biodiversity-productivity relationship. However, this relationship may break down in years with disturbance from drought or flooding, as evidenced by the higher productivity of Switch1 plots compared to other seed mixes in those years.

Productivity was affected differently by soil type in the two most diverse mixes. The Prairie32 mix had the highest mean yield of all mixes over four years on the loam soil, but produced the least biomass of all mixes over four years on the clay soil. Conversely, Prairie16 had the highest mean yield on the clay soil while producing the least on the loam soil. These two mixes produced similar amounts of biomass on the sand soil. While it is becoming clear that biodiversity increases ecosystem function at a large scale (Cardinale et al. 2007, Balvanera et al. 2006), it is also becoming evident that factors related to location (Hector et al. 1999, Balvanera et al. 2006) have large impacts on that relationship at smaller scales. The productivity of our most diverse plots shows that soil type is a factor in the relationship of planted species richness and productivity. These results suggest that the relationship between the species richness of a seed mix and biomass productivity may change with soil type, thus complicating the application of the BEF perspective of restoration.

Contrary to my hypothesis, increasing species richness from 16 to 32 significantly reduced biomass productivity on the clay soils. The composition of species in seed mixes may explain the different responses of Prairie 16 and Prairie32 to the soil types. While both mixes were dominated by indian grass, big bluestem and little bluestem, the Prairie16 mix contained 2.14 times the basal cover of ox-eye sunflower compared to

Prairie32 (Appendix B). Both the basal cover and biomass of C4 grass was greater in Prairie32 than Prairie16 (Appendix B, Appendix C). If C4 grasses or ox-eye sunflower differed in productivity due to soil type, these differences in composition of Prairie16 and Prairie32 may explain the difference in productivity between seed mixes due to soil.

Over four year, the seed mixes produced similar amounts of biomass. However, our study examined two years with rare disturbance events, the 12th largest flood crest of the Cedar River in 2013 and, the drought of 2012 that was 1.95 standard deviations below normal precipitation (NWS 2014, NOAA 2014). As our study only encompassed four years, disturbance events are over represented in this study. Additionally, the first year of the study, 2010, may have had reduced biomass production as only one year had passed after the site was planted. This suggests that the biomass productivity of 2011 may represent a better estimate of average biomass productivity over time or for similar diverse plantings in the region. If this is the case, long-term averages for species rich tallgrass plantings (16-32 species) may be closer to 12 Mg/ha instead of the 8 Mg/ha suggested by the average of the four years in this study, and possibly as high as 14 Mg/ha on soils with moderate corn suitability ratings, such as the clay and loam in our study. If 2011 is a more accurate representation of the long-term productivity of seed mixes, then our results support my hypothesis that increased planted species richness increases biomass productivity.

Resistance to Drought

Contrary to the predictions of BEF theory, Prairie16 and Prairie32 had significantly larger absolute declines in biomass production due to drought than WSgrass5 or Switch1. This conclusion is consistent with Pfisterer and others (2004), who experimentally induced drought in plots of the Swiss site of the BIODDEPTH experiment. They found larger impacts of drought on species rich grasslands than on lower diversity planting. Likewise, biodiversity was found to lower resistance to drought in a meta-analysis by Balvanera and colleagues (2006). These results are contrary to models which predict higher resistance in diverse communities (Tilman 1996; Yachi and Loreau 1999). My research provides additional supporting evidence that biodiversity does not provide increased resistance to drought. One explanation for the discrepancy between BEF models and experimental results is that the models assume there is little covariance in species' response to environmental variation (Yachi and Loreau 1999), but this may not be true in many situations (Hooper et al. 2005).

For Prairie16 and Prairie32, biomass production may resemble the productivity of a seed mix's dominant species in years with disturbance by drought or flooding. While Prairie16 and Prairie32, were less resistant to drought than Switch1 or WSgrass5, the biomass production of Prairie16 and Prairie32 in the drought year was similar to that of WSgrass5 (Figure 4). The same result was observed when the plots were disturbed by flooding in 2013 (Figure 4). WSgrass5, Prairie16, and Prairie32 mixes were more

similar in dominant species composition than Switch1 plots (Appendix B). The basal cover of these plantings were dominated by indian grass, big bluestem and little bluestem (Appendix B).

The mechanisms which cause the positive effects of biodiversity are placed in two categories. The selection effect, the effects caused by dominance of certain species, and complementarity effects, or positive species to species interaction (Hooper et al 2005). Our results suggest that complementarity effects may be stronger in years without disturbance, since diverse mixes produced more biomass in these years than the WSgrass5 mix which was dominated by the same three species as Prairie16 and Prairie32 (Appendix B). Also, selection effects may be stronger in years with disturbance by flooding or drought, as diverse plots produced similar amounts of biomass compared to WSgrass5. As Switch1 plots were drastically different in species composition than the other three seed mixes, it is reasonable that the biomass yields of Switch1 would respond differently to climatic variation than those of seed mixes with similar dominant species. Although Prairie16 and Prairie32 had lower resistance to drought, their productivity was only reduced to levels similar to that of a lower diversity mix dominated by the same species.

Resistance to Invasion

I predicted more species rich plantings would have less weed biomass than seed mixes with lower richness. I found that Switch1 plots had higher amounts of weed biomass than all other seed mixes across all years of the study. Similar levels of weed

biomass detected in WSgrass5, Prairie16 and Prairie32 suggests that high level of resistance to invasion by weeds can be achieved with few species, as little as five. The percentage of weed biomass to total biomass was low in all seed mixes and decreased through time until 2013 with disturbance by flooding. Weed biomass ranged from 6.1% in Switch1 to 1.8% in Prairie32 should be of little concern to many methods of processing biomass. However, switchgrass monocultures may require chemical suppression of weeds if invading woody species become a problem, thus decreasing the monetary and environmental profits of such crops. Our results suggest that high levels of resistance to invasion by weeds may be achieved with few species.

In the final year, Switch1 had the highest frequency of Siberian elm trees, *Ulmus pumila* (Appendix C). While woody species may be only minor problems when sites are annually harvested, they may be large problems for switchgrass monocultures if a harvest is missed due to poor weather or other factors.

Species rich communities may limit invasion because increased species richness may increase the chance that planted species and invading species occupy the same functional niche (Symstad 2000). We found that WSgrass5, consisting of only the C4 grass functional group, had similar resistance to invasion as Prairie16 and Prairie 32. This suggests that little functional diversity is necessary to achieve levels of invasion resistance similar to more species and functional group rich communities. This supports the conclusion of Farigone and colleagues (2003), who suggest C4 grass dominance may be more important in limiting invasion than the similarity of function between present and invading species.

Biomass Yields Compared to Other Studies

The results of this experiment confirm that above ground biomass yields from restored prairie plantings are regularly underestimated. Even the least productive soil produced 2.8 times more biomass than was recorded for harvests from conservation reserve program plantings in western Minnesota from 2009 to 2011 (2.5 Mg/ha, Jungers et al. 2013). The results from the Prairie32 (10.61 ± 1.12 Mg/ha) on loam soil (CSR 72) were similar to the results from Jarchow and Liebman's (2013) unfertilized plots containing 34 species (9.1 ± 1.0 Mg/ha) on soil with a CSR of 75. Additionally, I found biomass yields from low input plantings to be much higher, even on the low fertility sandy soil which averaged 7.68 ± 1.120 Mg/ha over four years, than estimates of 3.92 Mg/ha for native grassland used by the United States Department of Energy (DOE 2011).

Seed mixes in this study produced more biomass over time than most fertilized switchgrass cultivars grown in the region. Biomass yields from 'Cave in Rock' switchgrass plots in southern Iowa, USA, averaged 3.9 MG/ ha for unfertilized plots and 5.2 Mg/ ha for plots receiving 224 kg N/ha year from 1998 to 2002 (Lemus et al 2008). Even on the least fertile soil, the yields of the unfertilized seed mixes (from 6.18 to 7.68 Mg/ha) in this study exceeded those of fertilized switchgrass cultivars growing at a more southern latitude.

Another study examined yields from 1998 to 2001 of 20 fertilized cultivars of switchgrass on fertile (CSR 75) soil (Lemus et al 2002). Although the highest producing cultivar, 'Alamo', averaged 12.1 Mg / ha, similar to the biomass yields of diverse plots in 2011, only five of the fertilized cultivars had higher yields than the four year mean production of Switch1 and only three had higher yields than Prairie32. It should be noted that Lemus et al. (2002) grew the cultivars in small, 3x4.6 m plots. During this study, I observed strong edge effects especially on Switch1 and WSgrass5 plots. In switchgrass plots, plants near the edge of plots would commonly be larger than plants growing in the interior of the plot. This raises some skepticism of biomass yield estimates from small plots like those used by Lemus and colleagues (2002), as edge effects may lead to overestimation of possible yields under field conditions.

I found that, even with no fertilizer inputs, both switchgrass monocultures with diverse native genetics and species rich prairie plantings out produced many fertilized switchgrass cultivars in the region. While I expected diverse tallgrass prairie plantings to be as or more productive than fertilized switchgrass cultivars, the high productivity of Switch1 compared to fertilized cultivars of switchgrass monocultures was unexpected. One explanation for the high productivity of Switch1 compared to fertilized cultivars of switchgrass in the region is that we used genetically diverse, local-ecotype seed (Smith et al 2010) rather than switchgrass cultivars. Genetic diversity and local adaptation may lead to switchgrass plantings which are more productive than low-diversity fertilized

plantings. My results re-enforce Jarco and Leibman's (2013) conclusion that policy makers may severely underestimate the potential for diverse native plantings as productive energy crops.

Summary

With close to normal precipitation, species rich seed mixes may yield higher biomass productivity than species poor plantings. The effect of species richness on productivity may be complicated due to soil type. Doubling the species richness of Prairie16 on the clay soil significantly reduced biomass production, however, this is in contrast with the high productivity of the Prairie32 on loam soil. I found that increased species richness decreases resistance to drought, but increases resistance to weed invasion. I also note that all of the seed mixes were more productive than previous estimates for the yields of switchgrass or tallgrass species plantings in the region. Thus low input plantings are potentially competitive with fertilized switchgrass cultivars.

I recommend a seed mix that is similar to the Prairie16 or Prairie32 mix for the production of biomass, as these mixes may produce more biomass in years without disturbance by flooding or drought. However, producers should be aware of the strong interaction of soil type and seed mix which was detected in this study. When grown on appropriate soils these two mixes are expected to produce more biomass over time than grass-only mixes. Further exploration of diverse tallgrass plantings is needed to identify the cause of the differences in productivity in diverse mixes between soils. Currently, I suggest that the Prairie16 mix be used on soil types which are similar to the clay and sand

soil used in this study, while Prairie32 would be recommended for soils like the loam. Additionally, when high resistance to invasion by weeds is beneficial, Switchgrass monocultures should be avoided.

Conclusions

Testing predictions of biodiversity and ecosystem function in a field-scale restoration setting resulted in the following conclusions:

- Over four years including one-year post seeding, a flood year, and a drought year; Biomass productivity was similar in all seed mixes.
- Diverse mixes (16-32) may be more productive than mixes with few species in years without disturbance by drought or flooding.
- Productivity in the two most diverse mixes was affected differently by soil type and may be influenced by species composition.
- Plantings with higher species richness were less resistant to drought, but their productivity was only reduced to levels similar to that of a lower diversity mix dominated by the same species.
- High levels of weed resistance was achieved with five or more species in a planting.
- Unfertilized, genetically diverse switchgrass monocultures and diverse native tallgrass plantings produced more biomass than most fertilized cultivars of switchgrass grown in the region.

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APPENDIX A

CRITERIA FOR THE SELECTION OF SPECIES FOR PRAIRIE16

Prepared and evaluated by Dave Williams

1. Historic/Geographic Distribution – Only tallgrass prairie species, native to Iowa's pre-European landscape were chosen for this project. We believe that these plants, which have evolved with Iowa's climate and soils for 1000's of years, are the best-adapted plants for the state. In addition, we used only species with a statewide distribution. The best estimates of species distribution have been determined through observing local remnants and herbarium specimens (Christiansen and Muller, 1999. An Illustrated guide to Iowa Prairie Plants).
2. Productivity – Species were selected were based upon having a high amount of above ground biomass production. In preliminary investigations, we compared monoculture plantings of various prairie grasses and forbs, to determine which species had the highest above ground biomass production.
3. Availability of 'Source Identified' seed – We chose only species that were certified as 'Iowa Yellow Tag'. This ensured that genetics of the seed used for the project originated from Iowa prairie remnants.
4. Easily grown from seed – It is well known that some prairie species can be difficult to grow from seed. Since 1990, the Iowa Ecotype Project at the Tallgrass Prairie Center has been greenhouse growing many prairie species from seed for campus production plots. This process has given us the ability to determine which species are easy and difficult to grow from seed.
5. Standability – In order to maximize harvest of above ground biomass, vegetation has to be standing at the time of harvest so the hay mower can windrow the material. Harvesting times for prairie biomass have yet to be determined, but there is some evidence that harvesting prairie hay in late-winter/early spring rather than fall harvesting can reduce harmful minerals that cause slagging/fouling. Based upon observations of many planted prairies, we chose species that remained standing over-winter.
6. Adapted to various habitat types - Every plant species has evolved to grow within a certain range of soil moisture conditions. Iowa has 440 different soil types (Iowa Natural Resources and Conservation Service 2010). We chose species that have the broadest range of habitat types to maximize the potential for establishment and persistence for most Iowa locations.

7.Species phenology - Prairie plants have evolved to take advantage of available resources throughout the growing season. Generally, grasses and forbs that actively grow and flower in spring are not large biomass producing species as compared to species that actively grow and flower summer/early fall, so many of the species that were chosen for this project were from the latter group. In addition, with the goal of creating a plant community without the need for fertilizer, nitrogen fixing legume species were also included.

8.Life span – It has been observed that as a prairie planting matures, abundance of some species declines while abundance of other species increases. We chose species that can persist and increase in abundance as the planting matures.

9.Ability to co-exist with other species – We chose species that appeared to co-exist with the prairie grasses. This was determined by observation of mature prairie reconstructions that were originally planted with grasses and forbs. We avoided colonizing species that appear to reduce the abundance of other species growing around it. A good example of a colonizing species that was avoided was Canada goldenrod (*Solidago Canadensis*).

APPENDIX B

COMPOSITION OF SEED MIXES

I analyzed the composition of seed mixes using SIMPER in PRIMER 6 based on Bray-Curtis Dissimilarity. Data included each measurement taken from a plot from 2010-2013. Data were not transformed for this analysis. Over all soils, WSgrass5, Prairie16, and Prairie32 had more similar composition then Switchgrass1 (Figure B3, Table B3). Switchgrass was 93.75% dissimilar to WSgrass5, 96.54% dissimilar to Prairie16, and 97.01% dissimilar to Prairie 32 (Table B1). WSgrass5, Prairie16, and Prairie32 had pairwise dissimilarities ranging from 50.80% to 59.85% (Table B1).

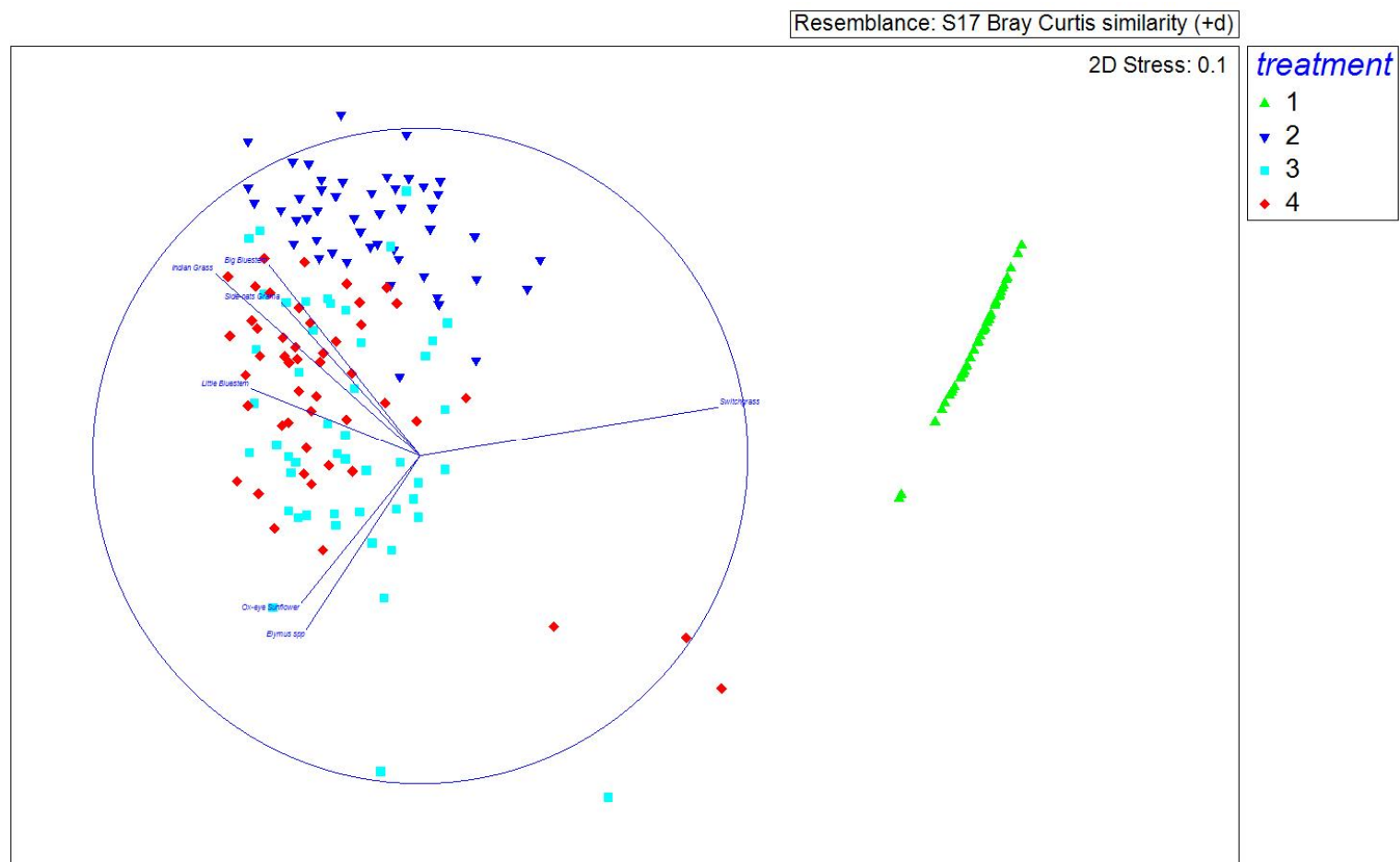


Figure B1: Non-metric Multidimensional Scaling of a Bray-Curtis resemblance matrix of basal cover estimates of planted species for each plot from 2010 to 2013. No transformation was applied to the basal cover data. The overlay shows species which are correlated with areas of the plot.

Table B1: SIMPER results based on Bray-Curtis Dissimilarity of basal cover data. Data included each measurement taken from a plot from 2010-2013. Data were not transformed for this analysis. Within and between group similarity/dissimilarity and the species which contribute highly to similarity/dissimilarity are listed.

Group Switch1

Average similarity: 81.73

Species	Av. Abund	Av. Sim	Sim/SD	Contrib%	Cum. %
Switchgrass	35.41	81.73	5.06	100.00	100.00

Group WSgrass5

Average similarity: 67.56

Species	Av. Abund	Av. Sim	Sim/SD	Contrib%	Cum. %
Big Bluestem	18.34	25.11	1.76	37.16	37.16
Indian Grass	14.41	24.31	2.40	35.99	73.16
Little Bluestem	8.06	10.05	1.16	14.87	88.03

Group Prairie16

Average similarity: 56.83

Species	Av. Abund	Av. Sim	Sim/SD	Contrib%	Cum. %
Big Bluestem	7.40	9.97	1.08	17.55	17.55
Indian Grass	6.91	9.41	1.38	16.57	34.12
Little Bluestem	5.25	9.13	0.96	16.06	50.18
Ox-eye Sunflower	5.27	8.48	1.19	14.92	65.10
Showy Tick Trefoil	3.31	5.83	1.31	10.25	75.35

Group Prairie32

Average similarity: 56.95

Species	Av. Abund	Av. Sim	Sim/SD	Contrib%	Cum. %
Indian Grass	8.86	14.03	1.95	24.64	24.64
Big Bluestem	8.65	10.78	1.24	18.93	43.57
Little Bluestem	4.36	5.80	0.91	10.18	53.75
Carex spp	2.52	4.57	0.91	8.02	61.78
Showy Tick Trefoil	3.02	4.00	1.32	7.03	68.81
Ox-eye Sunflower	2.46	3.57	1.06	6.27	75.07

Groups Switch1 & WSgrass5

Average dissimilarity = 93.75

	Group 1	Group 2				
Species	Av. Abund	Av. Abund	Av. Diss	Diss/SD	Contrib%	Cum. %
Switchgrass	35.41	2.70	39.54	2.95	42.17	42.17
Big Bluestem	0.00	18.34	21.33	1.83	22.76	64.93
Indian Grass	0.00	14.41	17.74	2.53	18.92	83.85

(table continues)

Groups Switch1 & Prairie16

Average dissimilarity = 96.54

Species	Group 1 Av. Abund	Group 3 Av. Abund	Av. Di ss	Di ss/SD	Contrib%	Cum. %
Switchgrass	35.41	1.26	46.24	3.70	47.90	47.90
Big Bluestem	0.00	7.40	9.08	1.24	9.41	57.30
Indian Grass	0.00	6.91	8.67	1.29	8.98	66.29
Little Bluestem	0.00	5.25	7.69	1.10	7.97	74.25
Ox-eye Sunflower	0.00	5.27	7.54	1.23	7.81	82.07

Groups WSgrass5 & Prairie16

Average dissimilarity = 59.85

Species	Group 2 Av. Abund	Group 3 Av. Abund	Av. Di ss	Di ss/SD	Contrib%	Cum. %
Big Bluestem	18.34	7.40	15.43	1.34	25.78	25.78
Indian Grass	14.41	6.91	11.92	1.42	19.91	45.70
Little Bluestem	8.06	5.25	6.66	1.12	11.12	56.82
Ox-eye Sunflower	0.00	5.27	6.26	1.17	10.47	67.28
Side-oats Grama	4.35	1.52	4.16	1.30	6.95	74.24
Showy Tick Trefoil	0.00	3.31	3.73	1.42	6.23	80.46

Groups Switch1 & Prairie32

Average dissimilarity = 97.01

Species	Group 1 Av. Abund	Group 4 Av. Abund	Av. Di ss	Di ss/SD	Contrib%	Cum. %
Switchgrass	35.41	1.06	43.78	3.43	45.13	45.13
Indian Grass	0.00	8.86	11.24	2.06	11.59	56.72
Big Bluestem	0.00	8.65	10.03	1.50	10.34	67.06
Little Bluestem	0.00	4.36	5.95	1.05	6.14	73.20
Showy Tick Trefoil	0.00	3.02	3.60	1.43	3.72	76.91

Groups WSgrass5 & Prairie32

Average dissimilarity = 56.90

Species	Group 2 Av. Abund	Group 4 Av. Abund	Av. Di ss	Di ss/SD	Contrib%	Cum. %
Big Bluestem	18.34	8.65	13.76	1.31	24.17	24.17
Indian Grass	14.41	8.86	9.01	1.23	15.83	40.01
Little Bluestem	8.06	4.36	6.70	1.17	11.77	51.78
Side-oats Grama	4.35	1.26	3.71	1.17	6.52	58.30
Showy Tick Trefoil	0.00	3.02	3.10	1.38	5.45	63.75
Carex spp	0.00	2.52	3.06	1.02	5.37	69.13
Switchgrass	2.70	1.06	2.78	0.90	4.88	74.00
Ox-eye Sunflower	0.00	2.46	2.72	1.16	4.78	78.79

(table continues)

Groups *Prairie16* & *Prairie32*
Average dissimilarity = 50.80

Species	Group 3 Av. Abund	Group 4 Av. Abund	Av. Diss	Diss/SD	Contrib%	Cum. %
Indian Grass	6.91	8.86	7.81	1.20	15.38	15.38
Big Bluestem	7.40	8.65	7.66	1.11	15.07	30.46
Little Bluestem	5.25	4.36	5.57	1.16	10.96	41.42
Ox-eye Sunflower	5.27	2.46	4.91	0.98	9.66	51.08
Carex spp	0.00	2.52	3.26	1.00	6.42	57.50
Stiff Goldenrod	1.91	1.59	2.75	0.88	5.42	62.92
Showy Tick Trefoil	3.31	3.02	2.69	1.23	5.30	68.21
Elymus spp	2.19	1.85	2.47	1.05	4.87	73.08
Yellow Coneflower	2.24	1.10	2.26	1.04	4.46	77.50

APPENDIX C

WEED COMPOSITION

Table C1: Most frequent weeds detected in each seed mix in 2013. For each species, numbers presented are total counts of presence in 20 0.1 m² quadrats per plot (240 total quadrats per seed mix).

	Switch1	WSgrass5	Prairie16	Prairie32	TOTAL
<i>Ulmus pumila</i>	132	18	11	2	163
<i>Solidago canadensis</i>	41	17	15	39	112
<i>Taraxacum officinale</i>	47	30	11	19	107
<i>Senecio plattensis</i>	17	9	12	16	54
<i>Poa pratensis</i>	18	12	16	7	53

Table C2: ANOVA table comparing *U. pumila* frequency between seed mixes in 2013. One-way ANOVA between seed mixes for natural log+1 transformed *U. pumila* counts (N=16). After transformation, data were normally distributed (Shapiro-Wilk p = 0.203) but had unequal variance (Levene's test p = 0.021).

	SS	df	MS	F-Ratio	p-Value
Seed Mix	32.194	3	10.731	26.573	<0.001
error	17.770	44	0.404		

Table C3: Pairwise comparisons of *U. pumila* frequency between seed mixes in 2013 using natural log+1 transformed *U. pumila* counts (N=16). Letters represent significant differences.

	Switch1	WSgrass5	Prairie16	Prairie32
mean	2.236 ^a	0.688 ^b	0.448 ^b	0.092 ^b

APPENDIX D

WARM SEASON GRASS

Warm season grass dominated the two functional group-rich seed mixes with 52.3% of the total biomass over the entire study. With weak statistical significance, the prairie mix had a higher proportion of warm season grass than the biomass mix (56% vs. 48%, $p = 0.068$, Table D1). The proportion of C4 grass increased significantly in 2012 and again in 2013 compared to prior years (Table D2). Warm season grass was also significantly more dominant on the sandy loam soil than the loam or clay loam soils over the four years (Table D2).

Table D1: ANOVA table for logit transformed proportions of warm season grass vs total plot biomass from 2010 to 2013.

Between subjects	SS	df	MS	Fratio	pvalue
Soil	11.510	2.000	5.755	6.474	0.008
Seedmix	3.354	1.000	3.354	3.773	0.068
Soil*Seedmix	0.395	2.000	0.197	0.222	0.803
Error	16.002	18.000	0.889		
within subjects					
Year	35.563	3.000	11.854	24.554	<0.001
year*Soil	5.960	6.000	0.993	2.057	0.074
year*Seedmix	0.679	3.000	0.226	0.469	0.705
year*soil*seedmix	1.765	6.000	0.294	0.609	0.722
Error	26.070	54.000	0.483		

Table D2: Proportion of warm season grass by year in prairie and biomass mixes, logit values, and lsd value. Letters represent significantly different groups.

years	C4grass	logit	LSD
2010	42.8%	0.322 ^a	0.278
2011	39.1%	0.553 ^a	0.278
2012	54.8%	0.216 ^b	0.278
2013	72.4%	1.029 ^c	0.278

Table D3: Proportion of warm season grass by soil in prairie and biomass mixes, logit values, and lsd values. Letters represent significantly different groups.

Soils	C4grass	Logit	LSD
loam	50.0%	-0.001 ^a	0.333
sand	62.2%	0.555 ^b	0.333
clay	44.6%	-0.277 ^a	0.333

APPENDIX E

MEAN BIOMASS PRODUCTION FOR SEED MIXES BY SOIL FOR EACH YEAR

Table E1: Mean biomass yield (Mg/ha) of each seed mix by soil for each year of the study (N=4).

2010	Switch1	WSgrass5	Prairie16	Prairie32
Loam	8.56	9.10	8.63	11.13
Clay	5.49	6.83	6.21	4.87
Sand	4.15	4.57	5.85	6.59
2011	Switch1	WSgrass5	Prairie16	Prairie32
Loam	10.46	10.12	11.65	14.30
Clay	11.87	9.40	14.57	12.23
Sand	8.75	8.82	9.88	9.53
2012	Switch1	WSgrass5	Prairie16	Prairie32
Loam	7.28	6.88	4.66	7.49
Clay	7.52	6.28	7.13	5.11
Sand	5.24	3.42	5.03	3.68
2013	Switch1	WSgrass5	Prairie16	Prairie32
Loam	11.53	8.87	8.49	9.51
Clay	8.89	7.74	7.03	5.31
Sand	9.55	7.88	9.95	8.98

APPENDIX F

PLOT LEVEL MEANS FOR EACH YEAR OF THE STUDY

Table F1: Yearly total means and functional group means for each plot. The column titles represent the following: WSG is the warm season grass functional group, CSG is the cool season grass functional group, FORB is non-leguminous forbs, LEG are plants in Fabaceae, and WEEDS are any plant not included in the seed mix planted in the plot. Units are g/m².

PLOT	YEAR	SOIL	SEEDMIX	WSG	CSG	FORB	LEG	WEEDS	TOTAL
A1	2010	Sand	Switch1	497.30	0.00	0.00	0.00	27.30	524.60
A1	2011	Sand	Switch1	1129.40	0.00	0.00	0.00	11.40	1140.80
A1	2012	Sand	Switch1	512.30	0.00	0.00	0.00	5.16	517.46
A1	2013	Sand	Switch1	699.87	0.00	0.00	0.00	4.39	704.26
A4	2010	Sand	Switch1	438.40	0.00	0.00	0.00	6.40	444.80
A4	2011	Sand	Switch1	890.80	0.00	0.00	0.00	10.30	901.10
A4	2012	Sand	Switch1	610.50	0.00	0.00	0.00	4.89	615.39
A4	2013	Sand	Switch1	837.47	0.00	0.00	0.00	60.85	898.32
C2	2010	Sand	Switch1	208.20	0.00	0.00	0.00	146.60	354.80
C2	2011	Sand	Switch1	645.40	0.00	0.00	0.00	39.70	685.10
C2	2012	Sand	Switch1	360.90	0.00	0.00	0.00	17.74	378.64
C2	2013	Sand	Switch1	1097.60	0.00	0.00	0.00	123.37	1220.97
C3	2010	Sand	Switch1	240.00	0.00	0.00	0.00	94.20	334.20
C3	2011	Sand	Switch1	735.90	0.00	0.00	0.00	36.60	772.50
C3	2012	Sand	Switch1	574.50	0.00	0.00	0.00	10.71	585.21
C3	2013	Sand	Switch1	981.63	0.00	0.00	0.00	14.77	996.40
F1	2010	Loam	Switch1	957.80	0.00	0.00	0.00	47.30	1005.10
F1	2011	Loam	Switch1	1123.00	0.00	0.00	0.00	10.30	1133.30
F1	2012	Loam	Switch1	806.70	0.00	0.00	0.00	5.58	812.28
F1	2013	Loam	Switch1	1155.27	0.00	0.00	0.00	59.55	1214.81
F2	2010	Loam	Switch1	700.50	0.00	0.00	0.00	64.80	765.30
F2	2011	Loam	Switch1	1310.00	0.00	0.00	0.00	25.00	1335.00
F2	2012	Loam	Switch1	603.10	0.00	0.00	0.00	9.57	612.67
F2	2013	Loam	Switch1	1106.60	0.00	0.00	0.00	71.50	1178.10
F3	2010	Loam	Switch1	672.70	0.00	0.00	0.00	126.90	799.60
F3	2011	Loam	Switch1	1213.10	0.00	0.00	0.00	25.40	1238.50
F3	2012	Loam	Switch1	726.80	0.00	0.00	0.00	20.89	747.69
F3	2013	Loam	Switch1	1109.17	0.00	0.00	0.00	71.50	1180.67
F4	2010	Loam	Switch1	728.30	0.00	0.00	0.00	124.90	853.20

table continues

[illegible]

H4	2011	Clay	Prairie32	1038.90	24.90	249.20	15.10	12.00	1340.10
H4	2012	Clay	Prairie32	260.66	11.92	47.16	173.47	2.70	495.91
H4	2013	Clay	Prairie32	656.90	15.00	34.59	52.37	21.15	780.01
H6	2010	Clay	Prairie32	146.60	34.00	287.40	54.40	3.80	526.20
H6	2011	Clay	Prairie32	692.60	57.20	295.40	206.70	21.10	1273.00
H6	2012	Clay	Prairie32	276.55	15.93	53.25	114.75	26.43	486.90
H6	2013	Clay	Prairie32	207.87	11.06	6.70	22.44	54.88	302.96